

# The Ant Larvae of the Subfamily Dolichoderinae: Supplement<sup>1</sup>

GEORGE C. WHEELER AND JEANETTE WHEELER

Department of Biology, University of North Dakota, Grand Forks

## ABSTRACT

An earlier study on the larvae of the Dolichoderinae was published by the authors in 1951. The present supplement contains descriptions of 9 additional species in the genera *Dolichoderus*, *Forelius* and *Iridomyrmex*. *Forelius* is new to the authors' collection and is characterized here for the first time. Necessary revisions are made in the 1951 descriptions and additional references to the literature are cited. The body profiles of dolichoderine

larvae are classified into 3 generalized types; there is only 1 generalized type of mandible shape. The tubercles of 6 genera (*Dorymyrmex*, *Iridomyrmex*, *Bothriomyrmex*, *Engramma*, *Tapinoma*, and *Technomyrmex*) are described and contrasted with the tubercles of ponerine larvae, from which they differ markedly in number, position and shape.

Subsequent to the publication of our article "The Ant Larvae of the Subfamily Dolichoderinae" (1951) we have received from other myrmecologists so much additional material that it seems desirable to publish a supplement.

In this article we describe the larvae of 1 genus and 9 species which we have acquired since 1951. Including these, we have studied a total of 45 species in 14 genera of this subfamily.

## REFERENCES TO THE SUBFAMILY<sup>2</sup>

Adlerz (1886) characterized the larvae as fat and capable of little movement (p. 275). After examining the larvae of *Tapinoma* he concluded—erroneously—that most of the hairs had been broken off and that further investigation would probably show that the dolichoderine larvae had double-hooked hairs (as in *Myrmica*) (p. 51).

Bernard (1951):—"Larves à tête petite, omnivores ou spécialisées; microcéphales, en boudin, poils rares" (p. 1041). "Leurs larves sont beaucoup moins mobiles et segmentées que celles des [Formicinae] . . . Les larves sont nues ou avec poils rares, à segmentation indistincte, à pièces buccales atrophiées ou nulles" (p. 1071).

Stärcke (1933):—"Larvae helpless. Strongly hypognathous. Few or no hairs; *Dolichoderus* has none; *Tapinoma* has hairs on the last segment; in *Iridomyrmex* they are generally distributed. Internal anatomy was also discussed.

## Tribe DOLICHODERINI Emery

### Genus *Dolichoderus* Lund

The very young larva (Wheeler and Wheeler 1951, pl. 30, Fig. 10) is similar to the mature larva except in the following details: Body ovoidal, with the head nearly the diameter of the prothorax and with the anterior end. Anus subterminal. Segmentation distinct. Body and head hairs reduced or lacking. Spinules on the integument isolated.

*Dolichoderus (Acanthoclinea) doriae* Emery (Fig. 3).—The immature larva (length through spiracles about 2.8 mm, straight length about 2.3 mm) is similar to *D. taschenbergi*, except in the following details: Body hairs moderately numerous, rather evenly distributed, longest ventrally. Integument with short rows of minute spinules. Cranium subrectangular in anterior view; broader than long. Head hairs numerous, longer (0.03–0.65 mm long). Labrum breadth 4 times the length; with a few short rows of minute spinules on the anterior surface. Mandibles with the basal half as broad as long. Maxillae with the apex adnate, the integument with short arcuate rows of minute spinules; palp represented by a cluster of 4 slightly elevated sensilla (3 with a spinule each). Labium with a few short rows of minute spinules; palp represented by 4 elevated sensilla (3 with a spinule each); an isolated sensillum between each palp and the opening of the sericteries.

The very young larva (straight length about 0.9 mm) is very similar to the immature larva.

Material Studied.—Numerous larvae from New South Wales, courtesy of the Reverend B. B. Lowery. This species is known also as *A. clarki* Wheeler.

Parasite.—In the sample of about 500 larvae, 47 contain 1 or 2 dipterous larvae, which are similar to those found in *Technomyrmex albigipes*. See Fig. 11, 12.

*Dolichoderus (Hypoclinea) mariae* Forel.—Length through spiracles about 2.9 mm, straight length about 2.5 mm. Similar to *D. taschenbergi*, except in the following details: Body hairs longer (0.018–0.036 mm long). Head hairs moderately numerous and longer (0.018–0.036 mm long). Antennae with 3 (rarely 4) minute sensilla, 2 (rarely 3) with a minute spinule each. Mandibles with the basal half about as wide as long and with a few minute spinules. Maxillae adnate, the integument with a few minute spinules; palp represented by 2 contiguous sensilla (1 encapsulated and 1 with a spinule); galea represented by 2 slightly raised sensilla each bearing a spinule. Labial palp represented by 2 contiguous sensilla; an isolated sensillum between each palp and the opening of the sericteries.

The sexual semipupa (length through spiracles about 4.7 mm, straight length about 3.6 mm) is simi-

<sup>1</sup> Accepted for publication October 26, 1965.

<sup>2</sup> The genus *Anacuretus*, established by Emery in 1892, has long been recognized as an adjunct between Dolichoderinae and the less specialized subfamilies. Clark (1951) removed the tribe Anacuretini from the Dolichoderinae and raised it to subfamilial rank as the Anacuretinae. Wilson et al. (1956) concurred, using larval characters (among others) to justify the separation (p. 87–89, 91, 93, 98; Fig. 3 on p. 86).

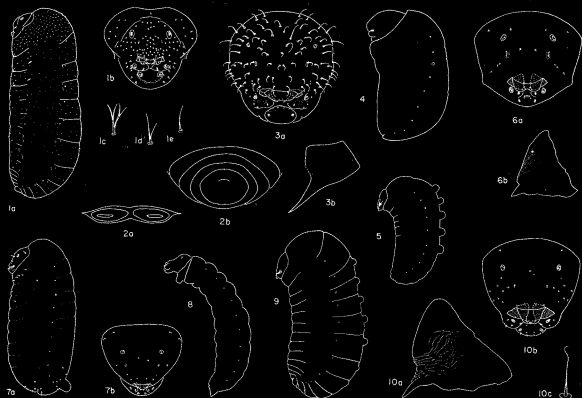


FIG. 1.—*Dolichoderus plagiatus*: a, larva, side view,  $\times 21$ ; b, head, anterior view,  $\times 50$ ; c-e, 3 body hairs,  $\times 423$ . FIG. 2.—*D. pustulatus*: a, intersegmental structure,  $\times 423$ ; b, ventral view, abdominal somites VII-X to show position of structure,  $\times 28$ . FIG. 3.—*D. doriae*: a, head, anterior view,  $\times 33$ ; b, left mandible, anterior view,  $\times 423$ . FIG. 4.—*D. bispinosus*: very young larva, side view,  $\times 44$ . FIG. 5.—*Froggattella kirbyi*: very young larva, side view (hairs omitted),  $\times 22$ . FIG. 6.—*Forelius brasiliensis*: a, head, anterior view,  $\times 111$ ; b, left mandible, anterior view,  $\times 423$ . FIG. 7.—*Tapinoma luteum*: a, immature larva, side view,  $\times 28$ ; b, head (immature larva), anterior view,  $\times 67$ . FIG. 8.—*Leptomyrmex pictus*: very young larva, side view (hairs omitted),  $\times 11$ . FIG. 9.—*Iridomyrmex punctatissima*: immature larva, side view (hairs omitted),  $\times 28$ . FIG. 10.—*I. gracilis*: a, left mandible anterior view,  $\times 423$ ; b, head, anterior view,  $\times 85$ ; c, body hair,  $\times 667$ .

lar to the worker larva, except in the following details: Body bean shaped, with the head anteroventral and the anus posteroventral. Body hairs about 0.035 mm long. Maxillary palp represented by 2 (rarely 3) encapsulated sensilla; galea with a stout spinule on each sensillum. Labium with a few isolated spinules; palp represented by 2 encapsulated sensilla.

Material Studied.—Eight larvae from Michigan, courtesy of Dr. Mary Talbot.

*Dolichoderus (Hypoclinea) plagiatus* (Mayr) (Fig. 1).—Length through spiracles about 3 mm, straight length about 2.4 mm. Similar to *D. taschenbergi*, except in the following details: Body straight, subcylindrical; no ventrolateral bosses on the prothorax. Wing vestiges present; gonopod vestiges present on abdominal somites VII, VIII, IX. Body hairs mostly 2- or 4-branched, a few simple. With integumentary structures of unknown nature and function in a row down each dorsolateral and ventrolateral surface, on most somites. Head hairs numerous; 0.01-0.02 mm long; simple or bifid. Maxillae adnate; with the apical portion spinulose, the spinules isolated or in arcu-

ate rows. Labium with an isolated sensillum between each palp and the opening of the sericteries.

The young larva (length through spiracles about 1.2 mm, straight length about 1 mm) has its head on the anterior end of the body. Otherwise it is very similar to the mature larva.

Material Studied.—Numerous larvae from Michigan, courtesy of Dr. Mary Talbot.

*Dolichoderus (Hypoclinea) pustulatus* Mayr (Fig. 2).—Length through spiracles about 2.8 mm, straight length about 2.5 mm. Similar to *D. taschenbergi*, except in the following details. Body similar to *D. plagiatus*. With a peculiar structure in the intersegmental membrane between abdominal somites IX and X (Fig. 2). Body hairs longer (0.01-0.025 mm long), simple or 2- or 3-branched. Head subtriangular in anterior view, widest at the antennal level; integument sparsely spinulose. Head hairs numerous, longer (0.02-0.04 mm long), simple or bifid. Labrum with the anterior and ventral surfaces bearing minute spinules in short rows. Maxillae with the apex spinulose, the spinules minute and in short rows. Labium

with a few short rows of minute spinules near the base; an isolated sensillum between each palp and the opening of the sericteries.

Material Studied.—12 larvae from Michigan, courtesy of Dr. Mary Talbot.

*Dolichoderus (Hypoclinea) quadripunctatus* (Linnaeus).—Torossian 1959: Proctodeal trophallaxis is observable during larval development; if a colony consists only of workers, the exchanges are released by the presence of second and third larval stages. Proctodeal food, produced exclusively by the workers, is the principal food of the larvae.

*Dolichoderus (Hypoclinea) taschenbergi* (Mayr).—The very young larva (straight length about 0.35 mm) has an ovoidal body. Head nearly the diameter of the body and on the anterior end. Anus subterminal. Segmentation distinct. Spiracles not uniform in size; first abdominal the largest, eighth abdominal the smallest. Integument sparsely spinulose, the spinules usually isolated. No body hairs seen. Head with the lateral borders and dorsal corners broadly rounded; mouth parts small. Antennae indistinct, each with 3 sensilla, each of which bears a spinule. No head hairs seen; integument of the head with a few spinules. Labrum indistinct; short and thick, breadth 4 times the length; ventral border nearly straight; 8 sensilla on and near the ventral border and 5 or 6 on each half of the posterior surface near the middle. Mandibles very small and feebly sclerotized; subtriangular in anterior view; no denticles seen. Maxillae feebly developed, apparently adnate; integument of the medial surface with a few short rows of minute spinules; palp represented by 2 or 3 sensilla; galea represented by 2 sensilla. Labium short and broad; sparsely spinulose, the spinules minute and isolated or in very short rows; palp represented by 2 sensilla; an isolated sensillum between each palp and the opening of the sericteries; the latter a short transverse slit.

The young larva (length through spiracles about 1.2 mm, straight length about 1.1 mm) is plump, chunky and nearly straight, with the ends rounded and lateral longitudinal welts prominent. Head on the anterior end. Anus ventral. Segmentation distinct. Spiracles not uniform in size; first abdominal largest, eighth abdominal smallest. Integument spinulose, the spinules usually in short rows. Body hairs present but sparse on the thorax and first 6 abdominal somites, most numerous on the prothorax; minute (0.005–0.025 mm long); simple. Head subtriangular in anterior view; with small depressed dorsolateral areas; mouth parts small. Head hairs few, simple, irregularly scattered, short (about 0.02 mm long). Antennae small, each with 3 sensilla, each bearing a spinule. Mandibles feebly sclerotized, subtriangular in anterior view, with denticles on the medial surface of the basal half. Maxillae with a few short rows of spinules on the medial surface. Labrum, maxillary palp, galea, labium, and hypopharynx similar to those of the mature larva.

Material Studied.—Numerous larvae from North Dakota.

*Dolichoderus (Monacis) bispinosus* (Olivier) (Fig. 4).—The very young larva (length through spiracles about 1.1 mm, straight length about 0.8 mm) is plump and without distinct segmentation; head on the anteroventral surface and about half the diameter of the prothorax. Anus posteroventral. Labrum breadth 5 or 6 times the length. Maxillary palp represented by 5 sensilla. Otherwise very similar to the very young larva of *D. taschenbergi*.

Material Studied.—4 larvae from the Panama Canal Zone, G. C. Wheeler, no. 355.

### Tribe LEPTOMYRMECINI Emery

#### Genus *Leptomyrmex* Mayr

*Leptomyrmex pictus* Wheeler.—Length through spiracles about 6.4 mm; straight length about 4.6 mm. Very similar to *L. erythrocephalus*, except in the following details: Wing vestiges present. With an irregularly folded area across the ventral surface in each intersegmental membrane; each ventrolateral surface with a row of integumentary structures on abdominal somites I–VIII. Cranium about as long as wide and with the sides parallel (in anterior view). Head hairs shorter (0.005–0.015 mm long). Mandibles with the apical third slender and jaggedly tapering to a sharp point; basal two-thirds with short rows of minute spinules, which are transverse on the anterior surface and oblique on the posterior surface. Maxillae adnate. Labium feebly bilobed.

The young larva (length through spiracles about 3.8 mm, straight length about 3.6 mm) is similar to the mature larva, except in the following details: Slender and arcuate. Body hairs very few on abdominal somites VII–X, where there are also isolated spinules. Mandibles with the apical third tapering to a slender point. See Fig. 8.

Material Studied.—Numerous larvae from New South Wales, courtesy of the Reverend B. B. Lowery.

### Tribe TAPINOMINI Emery

#### Genus *Froggattella* Forel

*Froggattella kirbyi* (Lowne).—Sexual larva (length through spiracles about 5.7 mm, straight length about 3.9 mm) has bean-shaped body and is without the dorsal row of bosses; otherwise similar to the worker larva.

The young larva (length through spiracles about 1.5 mm, straight length about 1.3 mm) is very similar to the mature larva, except in the following details: Dorsal surface with only 5 bosses (on the methathorax and abdominal somites I–IV), which are hemispherical; body more slender. See Fig. 5.

Material Studied.—Numerous larvae from New South Wales, courtesy of Rev. B. B. Lowery.

### Genus *Dorymyrmex* Mayr

*Dorymyrmex emmaericellus* (Kusnezov).—Marcus (1953, p. 31) claimed that the sex could be recog-

nized in pupae and young larvae by the number of antennal segments. But the antennae of ant larvae (and indeed the larvae of all Apocrita) are 1-segmented. Judged from his Fig. 12 (p. 33) he referred to the antennae of the pupa, which develop inside the head of the larva.

### Genus *Iridomyrmex* Mayr

The very young larva is similar to the mature larva, except as follows: Extremely stout and plump; curved ventrally; diameter decreasing rapidly from about the fifth abdominal somite to the posterior end; head on the anterior end and of nearly the diameter of the prothorax; 1 or more bosses on the middorsal line.

Stärcke 1933.—A swelling on the middle of the back; with thick integument and two sensilla.

*Iridomyrmex gracilis* (Lowne) (Fig. 10).—Length through spiracles about 2.1 mm; straight length about 1.4 mm. Similar to *I. pruinosus*, except in the following details: Body relatively shorter, ventral profile J-shaped; anus ventral. Gonopod vestiges present on abdominal somites VIII and IX. Integument with minute spinules in numerous short transverse rows on the ventral surface of the thorax and on the posterior somites. Body and head hairs about 0.02 mm long, with very slender tip. Cranium subtriangular in anterior view. Labrum with the breadth twice the length; bilobed due to an impression of the ventral border; anterior surface with 5 sensilla and a few short rows of minute spinules. Mandibles with the apical tooth slightly longer; basal portion with minute spinules arranged in rows; the rows short and longitudinal on the anterior surface, longer and radiating medially on the posterior surface.

Material Studied.—Numerous larvae from New South Wales, courtesy of the Reverend B. B. Lowery.

*Iridomyrmex humilis* (Mayr).—Torossian 1961.—Proctodeal trophallaxis is minimal in this species and is for larvae only. The droplets are small.

*Iridomyrmex itinerans* (Lowne).—Length through spiracles about 2.8 mm; straight length about 2.5 mm. Similar to *I. pruinosus*, except in the following details: Body relatively shorter, ventral profile J-shaped. Anus ventral. Integument with minute spinules in numerous short transverse rows on the ventral surface of the thorax and on the posterior somites. Labrum with the breadth twice the length; bilobed due to a median impression of the ventral border; anterior surface with 6 sensilla and a few transverse rows of minute spinules; posterior with about 6 sensilla in a median cluster. Mandibles with the apical tooth slightly longer; basal portion with minute spinules arranged in rows, the rows short and longitudinal on the anterior surface, longer and radiating medially on the posterior surface.

Material Studied.—Numerous larvae from New South Wales, courtesy of the Reverend B. B. Lowery.

*Iridomyrmex pruinosus* (Roger).—REVISION: The middorsal surface of the second abdominal somite bears a boss, which varies from distinct to barely distinguishable (this boss is present at all stages from

first-instar to the semipupa and varies independently of age).

CORRECTION: The head hairs are 0.012–0.018 mm long.

The first-instar larva (straight length about 0.45 mm) is similar to the mature larva, except as follows. Extremely stout and plump; curved ventrally; body nearly the same diameter throughout, slightly enlarged at the fourth and fifth abdominal somites; tapering rapidly to the round-pointed posterior end. Head anteroventral and of about the same diameter as the prothorax. Anus posteroventral. Body hairs shorter (about 0.01 mm long). Maxillae appearing adnate; palp a cluster of 5 sensilla on a slight elevation.

*Iridomyrmex punctatissimus* Emery (Fig. 9).—The immature larva (length through spiracles about 1.8 mm, straight length about 1.5 mm) is similar to *I. pruinosus*, except in the following details: Head less projecting. With a single row of middorsal bosses on the metathorax and abdominal somites I–IV. Labrum 3 times as broad as long. Mandibles with the basal portion spinulose, the spinules in rows, the rows short and longitudinal on the anterior surface, longer and radiating medially on the posterior surface. Maxillary and labial palps represented by raised clusters of 3 sensilla each (2 encapsulated and 1 with a spinule).

Material Studied.—Numerous larvae from New South Wales, courtesy of the Reverend B. B. Lowery.

*Iridomyrmex sanguineus* Forel.—Allee et al. mentioned (1949, p. 719) the predation of the moth larva *Cyclotrona monocentra* upon the larva of this ant.

### Genus *Bothriomyrmex* Emery

*Bothriomyrmex gibbus* (Soudek).—Bernard 1958, p. 408: "A Entreroches, j'ai été frappé par l'extrême agilité du *Bothriomyrmex* et surtout par la facilité de transport de ses larves: une ouvrière déplace une boule d'une quarantaine de larves, accrochées les unes aux autres par leurs poils. En moins de 3 minutes, toutes les larves sont rentrées dans les galeries du nid. Cela est un avantage dans la lutte pour la vie, la plupart des concurrents locaux mettant près d'un quart d'heure, sinon plus, pour abriter leurs larves et nymphes."

### Genus *Azteca* Forel

*Azteca longiceps* Emery.—The young larva is similar to the mature larva, except as follows: Posterior end narrowly round pointed; the terminal somites decreasing rapidly in size posteriorly. Head on the anterior end and of nearly the same diameter as the prothorax. See Wheeler and Wheeler 1951, pl. 32, Fig. 22.

### Genus *Forelius* Emery

Body hairs very few, simple, minute, and widely scattered. Head subhexagonal. Head hairs very few, simple, and minute. Mouth parts small. Labrum bilobed; with 4 sensilla on the anterior surface. Mandibles without teeth or denticles. Maxillae adnate;

without spinules; palp a cluster of 5 sensilla; galea a low knob bearing 2 sensilla. Labium short, broad, and rounded; palp a cluster of 5 sensilla.

*Forelius brasiliensis* Forel. (Fig. 6).—Body hairs few, simple, minute (about 0.005 mm long), widely scattered except on the ventral surface of the prothorax where they are moderately numerous. Head with rounded dorsal and ventral outlines and with ventrally converging cheeks. Head hairs minute (about 0.005 mm long), simple and very few. Antennae each with 3 sensilla, each of which bears a spinule. Mouth parts small. Labrum nearly 4 times as broad as long; bilobed owing to an impression of the ventral border; anterior surface with 2 sensilla each bearing a short spinule; ventral border with 2 sensilla and a few spinules; posterior surface with 6 sensilla on each half. Mandibles feebly sclerotized; subtriangular; as broad as long; apical sixth a narrow sharp-pointed tooth, basal five-sixths broad. Maxillae adnate; palp represented by a cluster of 5 sensilla (2 encapsulated and 3 with a spinule each); galea a low knob with 2 apical sensilla. Labium short, wide, and rounded; palp represented by a cluster of 5 sensilla (2 encapsulated and 3 with a spinule each); an isolated sensillum between each palp and the opening of the sericteries; the latter a transverse slit on the anterior surface between the tips of the maxillae. Hypopharynx densely spinulose, the spinules moderately long and in long rows, the rows grouped into 2 subtriangles which have their bases near the middle.

Material Studied.—1 damaged integument from Argentina, courtesy of Dr. N. Kusnezov.

#### Genus *Tapinoma* Förster

Adlerz 1886.—The larvae are stout and more or less cylindrical; they show movement only near the anterior end. When resting, the head is almost wholly withdrawn into the first body segment (p. 52). Internal anatomy, p. 58–64.

*Tapinoma erraticum* (Latreille).—Torossian 1960: The workers employ proctodael trophallaxis to a moderate extent in feeding the larvae.

*Tapinoma luteum* (Emery) (Fig. 7).—The immature larva (length through spiracles about 1.7 mm, straight length about 1.3 mm) is similar to *T. sessile* except in the following details: Body straight; head applied to the anteroventral surface; anus posterior; with a posterodorsal knob; about 5 distinct somites. Body hairs sparse, but more numerous on the prothorax and on the posterior somites. Head subtriangular. Head hairs scattered. Antennae larger and lower on the head. Labrum with the posterior surface sparsely spinulose, the spinules in a few arcuate rows. Maxillary and labial palps each represented by a cluster of 3 sensilla (1 large and 1 small encapsulated, 1 small bearing a spinule).

Material Studied.—2 larvae from Kenya, collected by Dr. N. L. H. Kraus.

*Tapinoma melanocephalum* (F.).—Stärcke (1933) stated that young larvae have large papillae on the

prothorax; in older larvae they are relatively much smaller. (We have not found such structures in other species.) He also described the posterodorsal knob and internal anatomy.

*Tapinoma nigerrimum* (Nylander).—Bernard 1951: Fig. 935A on p. 1018, larva in side view; Fig. 937B on p. 1020, internal anatomy (after Athias-Henriot).

*Tapinoma simrothi* Krausse.—Valentini 1951. Internal anatomy.

#### Genus *Technomyrmex* Mayr

We now believe that all our material (1951) is immature.

*Technomyrmex albipes* (F. Smith).—We now have numerous immature larvae from New South Wales (courtesy of the Reverend B. B. Lowery), which confirm our previous description (1951, p. 205).

Parasite.—In the sample of 114 larvae, 75 contain 1 or 2 dipterous larvae, which are similar to those found in *Dolichoderus* (*Acanthoclina*) *doriae*. See Fig. 11 and 12.

*Technomyrmex bicolor textor* Forel.—Forel and Jacobson 1909, p. 252: "Wenn der *Technomyrmex* wirklich der Erbauer des von ihm bewohnten Nestes ist, so stellt er die vierte Ameisengattung dar, die ihre Larven zum Spinnen und Weben verwendet." (Referred to by Wheeler in a footnote, 1915, p. 333.)

#### CHARACTERS

In our study (1960) of the larvae of the subfamily Myrmicinae we discussed the importance of various characters in taxonomy and described our techniques for generalizing about them. Applying the same reasoning and techniques to the larvae of the Dolichoderinae, we find 3 types of generalized mature body profiles (tubercles omitted).

1. **Dolichoderiform.**—Plump, chunky and slightly curved; subelliptical, with both ends broadly rounded; anterior end formed by the enlarged dorsum of the prothorax; head ventral, near the anterior end; no neck. Segmentation indistinct. Genera: *Aracomyrmex*, *Azteca*, *Bothriomyrmex*, *Dolichoderus*, *Dorymyrmex*, *Froggattella*, *Iridomyrmex*, *Tapinoma*.

2. **Leptomyrmeciform.**—Elongate, stout and slightly curved; diameter greatest at the third and fourth abdominal somites, decreasing rapidly toward either end. The 3 posterior somites small and directed ventrally. Prothorax sharply differentiated into 2 parts, the anterior part wedge-shaped (longer below) and abruptly depressed below the posterior portion. Head on the anterior end with the mouth parts directed anteriorly. Segmentation distinct. Genus: *Leptomyrmex*.

3. **Enggrammiform.**—Straight and subcylindrical; the posterior end slightly attenuated; anterior end formed by the dorsum of the prothorax; anterior portion of the prothorax forming a short stout neck, which is directed ventrally. Segmentation distinct. Genus: *Enggramma*.

In the subfamilies Myrmicinae (1960) and Ponerinae (1964) we found mature body shape to the character which was most nearly constant throughout the

\* *Forelius* and *Technomyrmex* are not included because we have only immature specimens; *Liometopum* is omitted because our material is unsatisfactory.

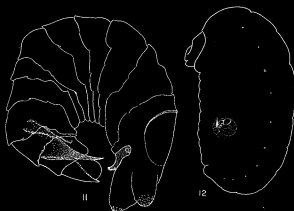


FIG. 11.—Dipterous parasite from *Technomyrmex albipes*,  $\times 176$ . FIG. 12.—Young larva of *D. dorae* containing larva of dipterous parasite,  $\times 27$ .

genus; it was also the character which most closely correlated larval taxonomy with adult taxonomy. Therefore, we chose mature body shape as the basic character for classifying the larvae of these 2 subfamilies. This character cannot be used, however, for the Dolichoderinae. The larvae of *Leptomyrmex* (like their adults) are highly aberrant, but the larvae of the tribes Dolichoderini and Tapinomini are similar in body shape (i.e., profile), except for *Engramma* which is distinct from other Tapinomini. See Fig. 13.

The mature mandible shapes, in contrast to the Myrmicinae and Ponerinae, fall into only 1 generalized pattern; see Fig. 14. In other words, the Dolichoderinae are a comparatively homogeneous group. To distinguish most of the genera, one must descend to trivial characters, such as hairs (size, shape, and abundance), tubercles, welts, and mouth parts.

#### HOMOGENEITY

Just how homogeneous are the larvae of the Dolichoderinae? To attempt an answer we have devised a simple index of heterogeneity: the ratio of the number of types of body profile (or mandible shape) to the number of genera studied; this index gives the

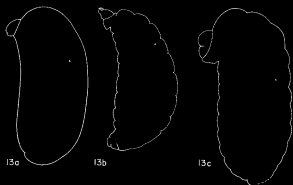


FIG. 13.—Generalized mature body profiles: a, dolichoderiform; b, leptomyrmeciform; c, engrammiform.

average number of genera per type. The lower the index the greater the heterogeneity.

Our computations follow:

#### PROFILES

Myrmicinae: 57 genera/22 types = 2.6  
Ponerinae: 26 genera/8 types = 3.3  
Dolichoderinae: 10 genera/3 types = 3.3

#### MANDIBLE SHAPES

Myrmicinae: 68 genera/30 types = 2.3  
Ponerinae: 33 genera/20 types = 1.7  
Dolichoderinae: 12 genera/1 type = 12.0

#### TUBERCLES

Many formicid larvae (in 30 out of the 168 genera studied) have 1 or more excrescences of some sort on the body. (See our 1964 article on Ponerinae for a general discussion.) To such structures the term "tubercle" has been applied. Since the shape varies greatly (e.g., low bosses, tall sharp spines) the term is not particularly appropriate, but nothing better has been suggested<sup>4</sup> and furthermore it has the sanction of long usage in myrmecology—Müller (1886), W. M. Wheeler (from 1900 on), Emery (Genera Insectorum, 1911). Therefore we shall continue to use it.

Tubercles are most frequently encountered in the Ponerinae (21 out of the 36 genera studied). Among the Dolichoderinae we have found them in 6 of 14 genera studied. Among the other subfamilies tubercles are rare (in 5 genera of 119 studied).

Except that they are all protuberances, dolichoderine tubercles have little in common with ponerine, differing in several respects:—(1) *In number*. Among the Ponerinae the number of tubercles per larva ranges between 10 and 400, although the count for most genera lies between 100 and 200. Among the Dolichoderinae the number ranges from 1 to 8. (2) *In position*. In the Ponerinae the tubercles are generally distributed over the dorsal and lateral surfaces, while dolichoderine tubercles have been found only at or near the posterior end or on the dorsal surface or on the ventral surface of the prothorax. (3) *In shape*. Although ponerine tubercles vary greatly in form, the majority are either spinelike or bear stout hairs, and could conceivably serve as defensive function. Dolichoderine tubercles lack hairs, are never

<sup>4</sup> Brown (1963, p. 5) has proposed that the term "chalaza" be substituted for "tubercle." The Greek word *chalaza* means "hail" or "pimple" and is therefore no more appropriate than "tubercle." Furthermore, it already has restricted meanings in botany and in avian embryology.

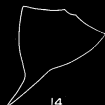


FIG. 14.—Generalized mature mandible shape for the subfamily Dolichoderinae.

spinellike, and, for the most part, are smoothly rounded.

The following list summarizes the tubercles we have found in the subfamily Dolichoderinae. The structures are most conspicuous in young larvae, but since they remain the same size they become relatively smaller and therefore less conspicuous as the larva grows.

*Dorymyrmex*. A slender subconical tubercle at the posterior end.

*Iridomyrmex*. 1-5 rounded bosses (1/somite) along the middorsal line.

*Bothriomyrmex*. Prothorax with a pair of antero-ventral bosses. In the young larva of 1 species each boss is produced into a fingerlike process.

*Engramma*. Paired dorsal bosses, which are more prominent anteriorly, and a conspicuous knob at the posterior end.

*Tapinoma*. A rounded posterodorsal boss.

*Technomyrmex*. A rounded posterodorsal boss.

#### REFERENCES CITED

- Adlerz, G. 1886. Myrmekologiska studier II. Svenska myror och deras lefnadsförhållanden. Bihang K. Svenska Vet.-Akad. Handl. 11: 1-329.
- Allee, W. C., A. E. Emerson, O. Park, T. Park, and K. P. Schmidt. 1949. Principles of Animal Ecology. W. B. Saunders Co., Philadelphia. 837 p.
- Bernard, F. 1951. Super-famille des Formicoidea. In: P. P. Grassé, ed., Traité de Zoologie, Tome X, Fasc. II: 997-1104. Masson et Cie, Paris.
1958. Notes écologiques et biologiques sur une fourmi parasite nouvelle pour la France: *Bothriomyrmex gibbus* (Soudek). Bull. Soc. Zool. France 83: 401-9.
- Brown, W. L. 1963. Characters and synonymies among the genera of ants. Part III. Some members of the tribe Ponerini. Breviora Mus. Comp. Zool. Harvard Univ. no. 190. 10 p.
- Clark, J. 1951. The Formicidae of Australia. Vol. I. Subfamily Myrmecinae. Commonwealth Sci. Indust., Res. Organ. (Melbourne, Australia). 230 p.
- Forel, A., and E. Jacobson. 1909. Ameisen aus Java und Krakatau beobachtet und gesammelt von Edward Jacobson. I. Theil. Notes Leyden Mus. 31: 221-53.
- Marcus, H. 1953. Estudios mirmecológicos. Folia Universitaria (Cochabamba, Bolivia) no. 6: 17-68.
- Stärcke, A. 1933. Over de larven der dolichoderinen. Tijdschr. Entomol. 76: XXVI-XXXII.
- Torossian, C. 1959. Les échanges trophallactiques proctodéaux chez la fourmi *Dolichoderus quadripunctatus*. Insectes Sociaux 6: 367-74.
1960. Les échanges trophallactiques proctodéaux chez la fourmi: *Tapinoma erraticum*. Insectes Sociaux 7: 171-4.
1961. Les échanges trophallactiques proctodéaux chez la fourmi d'Argentine: *Iridomyrmex humilis*. Insectes Sociaux 8: 189-91.
- Valentini, S. 1951. Sur l'adaptation des larves de Formicoidea. Ann. Sci. Nat. (Zool.) 11: 249-76.
- Wheeler, G. C., and J. Wheeler. 1951. The ant larvae of the subfamily Dolichoderinae. Proc. Entomol. Soc. Wash. 53: 169-210.
1960. The ant larvae of the subfamily Myrmicinae. Ann. Entomol. Soc. Amer. 53: 98-110.
1964. The ant larvae of the subfamily Ponerinae: supplement. Ann. Entomol. Soc. Amer. 57: 443-62.
- Wheeler, W. M. 1915. On the presence and absence of cocoons among ants, the nest-spinning habits of the larvae and the significance of the black cocoons among certain species. Ann. Entomol. Soc. Amer. 8: 323-42.
- Wilson, E. O., T. Eisner, G. C. Wheeler, and J. Wheeler. 1956. *Aneuretus simoni* Emery, a major link in ant evolution. Bull. Mus. Comp. Zool. Harvard Univ. 115: 81-99.

Reprinted from the

ANNALS OF THE ENTOMOLOGICAL SOCIETY OF AMERICA

Volume 59, Number 4, pp. 726-732, July 1966